Assessing the Rate, Mechanisms, and Consequences of the Conversion of Tallgrass Prairie to *Juniperus virginiana* Forest

John M. Briggs,[2]** Greg A. Hoch,[1]* and Loretta C. Johnson[1]

[1]Division of Biology, Kansas State University, Manhattan, Kansas 66502, USA; [2]Department of Plant Biology, Arizona State University, Tempe, Arizona, USA

ABSTRACT

We assessed the determinants and consequences of the expansion of *Juniperus virginiana* L. (red cedar) populations into central US grasslands using historical aerial photos and field measurements of forest extent, tree growth, fire-induced mortality, and responses in herbaceous species diversity and productivity. Photos from northeast Kansas dating back to 1956 indicate that native tallgrass prairie can be converted to closed-canopy red cedar forest in as little as 40 years (a 2.3% increase in forest cover per year). Mean tree density in 21 forested sites ranged from 130 to 3500 trees/ha, with most sites at more than 800 trees/ha. In younger stands, maximum growth rates of individual red cedar trees exceeded 20 cm/y in height. Land management practices were critical to the establishment and growth of red cedar forest. Grazing reduced the fuel loads by more than 30% in tallgrass prairie. Based on measurements of mortality for more than 1800 red cedar

trees, fire-induced mortality in grazed areas averaged 31.6% versus more than 90% at ungrazed sites. When tallgrass prairie was converted to red cedar forest, herbaceous species diversity and productivity were drastically reduced, and most grassland species were virtually eliminated. Consequently, community structure shifted from dominance by herbaceous C_4 species to evergreen woody C_3 species; this shift is likely to be accompanied by alterations in carbon storage and other ecosystem processes in a relatively short time period. Here we present a conceptual model that integrates the ecological and socioeconomic factors that underlie the conversion of grassland to red cedar forest.

Key words: forest expansion; *Juniperus virginiana*; tallgrass prairie; land-cover change; land-use change; fire; grazing; red cedar.

INTRODUCTION

Over the past several decades, woody species have invaded and displaced grasslands in Australia (Brown and Carter 1998), Africa (Moleele and Perkins 1998), and South America (Dussart and others 1998). In North American grasslands, this phenom-

enon has been described in mesic tallgrass prairies of the eastern Great Plains (Beilmann and Brenner 1951; Bragg and Hulbert 1976), desert grasslands of the Southwest (Schlesinger and others 1990), and the upper Great Basin (Miller and Rose 1995). The expansion of woody species in North America at the expense of native grasslands has been attributed to a number of individual factors, such as (a) the elimination of fire (Bragg and Hulbert 1976; Blewett 1984); (b) intensive grazing, usually by domestic livestock (Archer 1989; McPherson and others 1988; Schmidt and Stubbendieck 1993; Scholes and

Archer 1997); and (c) climate change (Idso 1992; Archer and others 1995). However, interactions among multiple factors, such as fire and grazing, are likely to be important as well (Leopold 1924; Johnsen 1962; Ellis and Schuster 1968; Blackburn and Tueller 1970; Burkhardt and Tisdale 1976; Madany and West 1983; Arno and Gruell 1986; Steinauer and Bragg 1987; Miller and Rose 1995).

The end points of invasions of grasslands by woody species can take two forms, both of which have serious ecological consequences. The large-scale mesquite/larrea invasion of arid and semiarid grasslands in Texas and New Mexico is a well-documented example of the changes that take place when grasslands are converted to systems dominated by woodland/grass (that is, savanna) (Archer and others 1988; Schlesinger and others 1990). An even more extreme conversion occurs in mesic grasslands, where grasses can be completely replaced by closed-canopy forest (Bragg and Hulbert 1976; Hoch and Briggs 1999). Earlier studies in mesic tallgrass prairie (Abrams 1986; Knight and others 1994) documented the expansion of oak forests into grasslands, but this expansion was limited to lowlands along watercourses. However, a native tree species, *Juniperus virginiana* L., may pose more of a threat to tallgrass prairie, since it can expand into both lowland and uplands within the grassland (Owensby and others 1973; Engle and Kulbeth 1992).

Juniperus virginiana (hereafter referred to as "red cedar") is one of the most widely distributed tree species in the eastern United States, occurring in every state from the eastern Great Plains to the Atlantic Coast (Van Haverbeke and Read 1976). Red cedar is characterized by rapid growth, high reproductive output, and widespread dispersal of seeds by birds (Holthuizjen and Sharik 1985). The impacts of red cedar expansion in North America have been studied from coarse spatial scales using forest inventory data (Schmidt and Leatherberry 1995) to the fine-scale quantification of productivity and diversity under isolated trees (Engle and others 1987; Smith and Stubbendieck 1990; Gehring and Bragg 1992).

However, a comprehensive assessment of the rate of red cedar expansion and its ecological impact is needed to gain a better understanding of the causes and consequences of this process. Therefore, the purpose of this study was to (a) quantify the rate of conversion of tallgrass prairie to closed canopy red cedar forest; (b) characterize different-aged red cedar forests by tree size and density; (c) quantify the growth rate of individual trees; (d) examine plant community responses, in terms of herbaceous pro-

ductivity and diversity, to this grassland–forest conversion; and (e) assess how grazing and fire interact to determine red cedar mortality. Finally, the socioeconomic factors that influence this conversion are considered.

METHODS

Study Area

This study was conducted in the northern end of the Flint Hills region of east-central Kansas (39°N, 96°W). Earlier analysis of satellite imagery (Hoch and Briggs 1999) determined that the extent of expansion of red cedar forest was higher in this area than in surrounding areas. The Flint Hills region is a 70-km–wide band of gently rolling hills stretching from the Nebraska border south into Oklahoma. The Flint Hills are underlain by a series of limestone and shale formations that form characteristic outcrops, or "breaks", on the hillsides. Due to the steep topography and rocky soils, much of this region was never plowed and thus contains some of the largest tracts (1.2 million ha total) of tallgrass prairie remaining in the world (Samson and Knopf 1994). Grasslands here are dominated by C_4, or warm season, grasses, specifically big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparius*). Riparian forests are dominated by bur and chinquapin oaks (*Quercus macrocarpa* and *Q. muhlenbergii*). Row crop agriculture dominates the deeper, permeable soils along major drainages.

Five red cedar forests in this area, which had a mature canopy in 1996, were measured from aerial photos dating from 1956, 1969, 1978, 1985, and 1996 to quantify rates of expansion (two of these five forests are sites 4 and 5 in Table 1). These sites were chosen based on their representation of the invasion of red cedars into grasslands in this area, the availability of high-quality aerial photographs, accessibility for ground truthing, and their maturity. A transparent dot grid overlay (Lillesand and Kiefer 1994) was placed over randomly selected 1-ha areas in the five sites. The number of dots covering red cedar trees was counted to determine the percent aerial coverage for each site and time. The five sites were combined to estimate the average coverage for each time period. Extensive ground truthing in the summer of 1998 revealed that the discriminations of the 1996 images were more than 95% accurate. The percent of red cedar canopy at each date was calculated to determine the rate at which open grassland was converted into closed-canopy red cedar forest.

Table 1. Results of Survey of 18 Red Cedar Forests in Riley County, Kansas

Site	Aspect	Soil Mapping Unit	n	Mean DBH (cm)	Max DBH	Trees/ha	Slope	Intercept	r^2
1	NW	Clime-Sogn	20	23.9 (1.1)	47	803.3	0.58	−3.17	0.92
2	W	Clime-Sogn	20	13.5 (1.9)	40.5	840.2	0.96	−13.6	0.98
3	Flat	Clime-Sogn	4	9.7 (0.9)	30.1	2214.5	0.92	−7.9	0.93
4	Flat	Clime-Sogn	20	18.6 (1.0)	36	1527.6	0.32	−1.1	0.35
5	Flat	Benfield-Florence	20	17.4 (1.0)	29.8	1720.2	0.42	−2.9	0.57
6	SE	Benfield-Florence	4	9.0 (0.7)	20.1	1932.1	0.94	−3.7	0.96
7	E	Clime-Sogn	4	17.9 (1.0)	27.5	130.6	1.41	−22.9	0.96
8	Flat	Clime-Sogn	4	10.5 (0.8)	21.5	976.6	0.9	−6.53	0.90
9	W	Clime-Sogn	4	14.1 (1.3)	40.3	580.6	1.06	−11.5	0.69
10	S	Clime-Sogn	20	7.1 (1.0)	22.5	354.3	0.63	0.82	0.89
11	S	Benfield-Florence	4	12.8 (1.2)	25.1	380.7	0.98	−3.01	0.96
12	Flat	Clime-Sogn	4	7.5 (0.7)	18.3	522.4	0.79	−1.64	0.75
13	Flat	Benfield-Florence	4	9.5 (1.0)	28	3787	0.62	−0.38	0.93
14	E	Benfield-Florence	4	14.7 (1.3)	26.3	826.1	0.468	−0.72	0.44
15	Flat	Clime-Sogn	4	13.0 (1.1)	25.9	2066	0.82	−3.86	0.95
16	S	Stony steep	4	12.5 (1.0)	27.2	142.5	0.85	−5.65	0.87
17	E	Clime-Sogn	4	13.3 (0.6)	27.5	3564.3	0.78	−1.27	0.57
18	W	Stony steep	20	14.3 (1.5)	32.5	7243.1	1.01	−7.66	0.83

Aspect, soil mapping unit, and number of trees cored (n) are reported. Mean DBH (diameter at breast height), maximum DBH, and tree density (trees/ha) are also reported. Allometric relationships (DBH versus age or height versus age), as well as amount of variance explained in the relationship (r²), are also reported.

Forest structure was determined from 21 red cedar stands, ranging in age from less than 10 years to more than 70 years; 15 of these forests had a closed canopy. These stands were selected to capture a range of red cedar forest ages in the area and to represent the general pattern of grassland invasion by red cedars in the region. At each site, 10 random points were established; the points were set at least 10 m apart to ensure that no trees would be sampled twice. The point-quarter method (Dix 1961) was used to measure tree density. Density was determined using the following equation:

$$\text{Density (trees/ha)} = 1/(\text{average distance[m]})^2$$
$$\times 10,000$$

Diameter at breast height (DBH) was measured for each of four trees in the cardinal directions at each point (40 trees per site). Increment cores were taken from four of the 40 trees to develop size-age relationships for each site (Table 1). Skeleton plots (Stokes and Smiley 1996) were used to identify false rings, a common problem in this species. The soil mapping unit for each forest was determined from the USDA Soil Survey (Jantz and others 1975).

Nine of the 21 sites, ranging from the youngest to the oldest, were selected for more intensive study. Three sites represented the oldest forest stands

(35–70 years); three sites had trees more than 2 m tall, but the canopy had not yet closed; and three sites represented young forests where the trees were spaced widely and less than 2 m tall. At 10 random points, a 10-m^2 circular plot was established, and all plant species within this plot were identified to species. Species richness was censused twice in 1998, once in mid-June, and again in late August to ensure that both early- and late-flowering species could be identified. Species richness was plotted as a function of tree density at each point. A Student's t-test was used to compare species richness in points below the red cedar canopy and points in the adjacent grassland. At these sites, increment cores were taken from two trees at each point (20 cores/site) to develop more robust size-age relationships (Table 1). At the three young sites, two trees per point were cut at ground level and a disk of wood removed to develop age-height relationships for small trees (Table 2). Trees were cut after the second sampling date.

Based on censuses for species richness, the time for peak biomass for the most common understory species in red cedar forests was determined to be in late May. At this time, all vegetation was harvested from 15 0.1-m^2 quadrats randomly located at site 4 (Table 1). These values were then compared to biomass values on annually burned ungrazed watersheds at nearby (less than 15 km) Konza Prairie

Table 2. Results of Survey of three Red Cedar Forests in Riley County, Kansas

Sites	Aspect	Soil Type	n	Slope	Intercept	r^2
19	Flat	Clime-Sogn	20	1.55	−3.09	0.49
20	Flat	Clime-Sogn	20	0.92	−1.49	0.24
21	Flat	Clime-Sogn	20	1.15	−2.19	0.11

Aspect, soil mapping unit, and number of trees cored (n) are reported. Allometric relationships (DBH versus age or height versus age), as well as the amount of variance explained in the relationship (r^2), are also reported. Sites 19, 20, and 21 were the three young sites where two trees per point were cut at ground level and a disk of wood removed to develop age-height relationships for these smaller trees. Trees were harvested after the second sampling date.

Biological Station (KPBS) using data from the KPBS Long-Term Ecological Research (LTER) program (www.konza.ksu.edu) on similar topographic positions and soils. The effects of fire and fire-grazing interactions on the mortality of red cedar trees were assessed at four sites with established red cedar populations. Trees at these sites ranged in size from seedlings to mature trees more than 2.5 m tall. Two sites had not been grazed for 3 years prior to 1999; the other two sites have been grazed annually for at least 5 years. Stocking rates at the two sites were approximately 3.4 animal-unit-months/ha, and both areas were grazed until early November 1998. All four sites were burned during the 2nd week of April 1999. None of the sites had been burned for 3–4 years prior to this study.

During the summer of 1999, 1869 trees were sampled. At least 400 trees were sampled per site. The height of the tree was recorded, as well as whether the tree was living or dead. Trees were recorded in 0.2-m size classes from 0.5 to 2.8 m. If the trees had any green branches (not completely top-killed), they were recorded as live.

The potential fuel load on the ungrazed and grazed sites was estimated from herbaceous biomass data obtained from annually burned sites on KPBS (less than 1 km from the two ungrazed sites and approximately 5 km from the grazed sites). Thirty 0.1-m^2 quadrats were harvested from a grazed and an ungrazed area on KPBS in late summer of 1998. The samples were air-dried and weighed using the protocol described in Knapp and others (1998).

RESULTS

Analysis of aerial photos from five forests (see Figure 1) in the Flint Hills of eastern Kansas indicated that red cedar can expand and convert tallgrass prairie to a closed-canopy forest in as little as 40
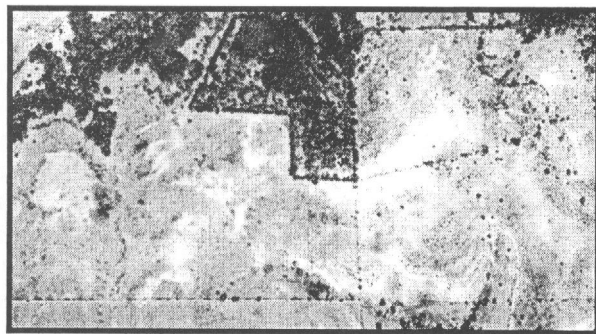
years. The maximum expansion rate was 5.8% per year between 1969 and 1978. Overall, a sigmoid growth curve best described forest expansion and maturation (Figure 2). Based on tree core data, two of the five forests (sites 4 and 5 in Table 1) on which this analysis was conducted were among the oldest forests in this region and included trees estimated to be more than 35 years old. Thus, the coring data supported our interpretation of the aerial photos.

A total of 172 increment cores were taken across all sites. The relationship between DBH and tree age (based on ring counts) included data from 172 trees cored and was strong for most sites (r^2 greater than 0.85) (Tables 1 and 2). However, the height–age relationships for the three youngest sites ($n = 60$ for all three sites) were not as robust (r^2 ranging from 0.11 to 0.49) (Table 2), perhaps reflecting the importance of differences among sites in determining initial growth rates. Overall, mean DBH for most forests was less than 20 cm (Tables 1 and 2); mean tree density varied from 130 to 3500 trees/ha, with most more than 800 trees/ha. At the youngest sites, red cedar trees grew at a rate of 20 cm/y in height (Table 2).

There was a significant negative relationship between species richness and tree density ($r^2 = 0.56$, $P < 0.0001$) (Figure 3). Similarly, plots underneath the red cedar canopy had significantly fewer herbaceous species than plots outside the canopy ($t = 17.01$, $P < 0.0001$) (Figure 3 inset). Herbaceous species commonly found in the closed-canopy sites included Kentucky bluegrass (*Poa pratensis*), western yarrow (*Achillea millefolium*), and bedstraw (*Galium* spp.). However, there were no species that were found consistently in the understory of these forests or that were distinct from those species present in the adjacent grasslands. In red cedar forests contiguous with deciduous forests (three sites), bur oak (*Quercus macrocarpa*), hackberry (*Celtis occidentalis*), redbud (*Cercis canadensis*), and mulberry (*Morus alba*) seedlings were found. Saplings from deciduous species were rare in these forests, however, and were only present at the forest edge. Only two red cedar seedlings were found in the plots sampled under a mature red cedar canopy; no other woody species were observed.

Understory biomass, including herbaceous vegetation and woody seedlings, averaged 0.18 ± 0.10g/m^2 in red cedar forests; whereas on annually burned watersheds at KPBS, herbaceous production was 384 ± 16 g/m^2. Thus, as compared to tallgrass prairie, herbaceous production in a red cedar forest was decreased by over 99%.
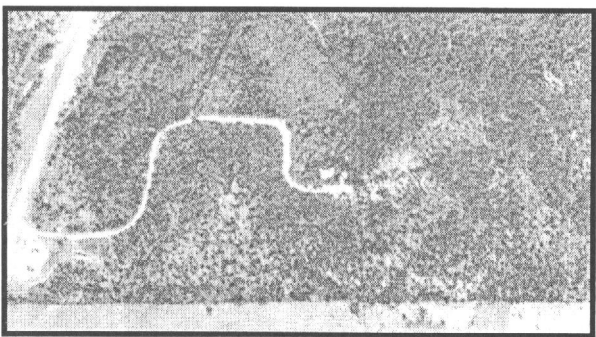
Herbaceous biomass at the end of the 1998 growing season was 249 ± 7 g/m^2 and 374 ± 15 g/m^2 in
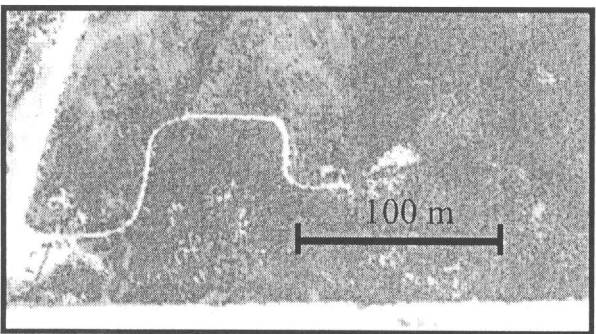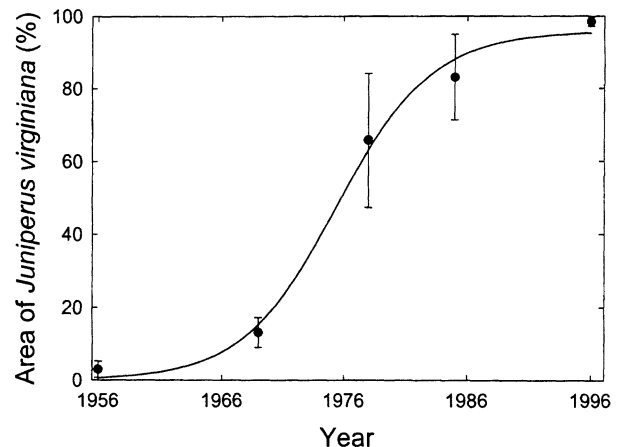
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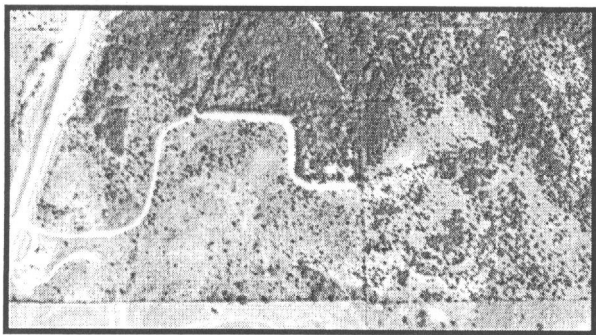
1969

1978

1995

Figure 2. The average rate of expansion of five red cedar forests. Areas were clipped from aerial photographs of the forest, and red cedar densities were measured using the dot overlay method. The percentage of the areas that were red cedar is plotted against time to determine the rate of red cedar canopy expansion. Between 1969 and 1978, the maximum expansion rate was 5.8% per year. Overall, a sigmoid growth curve best described forest maturation. Error bars-one standard error of the mean (SEM).

the annually burned grazed and ungrazed watersheds on KPBS, respectively. Analysis of variance (ANOVA) revealed no differences in red cedar mortality between sites under the same treatment (grazed and ungrazed); therefore, the sites were combined for statistical analysis. Grazing reduced the potential fuel loads by 33%, and this reduction had a significant effect on red cedar mortality. For example, in ungrazed sites, tree mortality averaged 94% ($\pm$ 1.8 standard error [SE]); whereas in grazed sites, mortality was only 32% ($\pm$ 6.4 SE). In the ungrazed areas, trees in the smallest size classes (0.6–1.4 m) had a 100% mortality rate and even the largest class (2.8 m) averaged over 80%; whereas in the grazed areas, the size class of 0.6–1.4 m had average mortality rates of less than 65% and trees taller than 2 m had rates less than 20% (Figure 4).

Figure 1. A series of four aerial photos dating to 1956 showing the expansion rate of the red cedar forests (*dark areas*) into tallgrass prairie (*light gray areas*). Note the dramatic increase in red cedar between 1969 and 1978. Also note the straight fence lines, which demonstrate the importance of management practices on red cedar expansion.
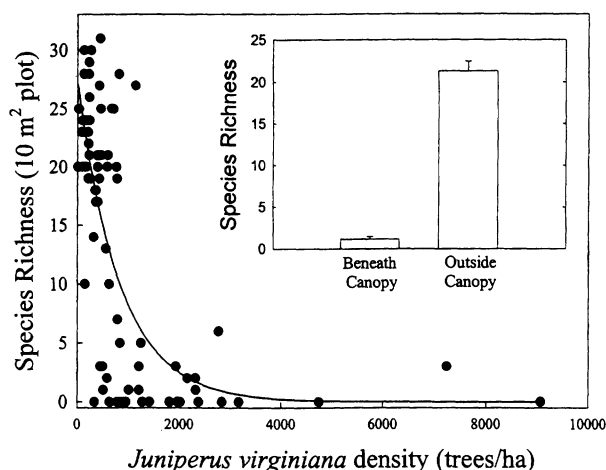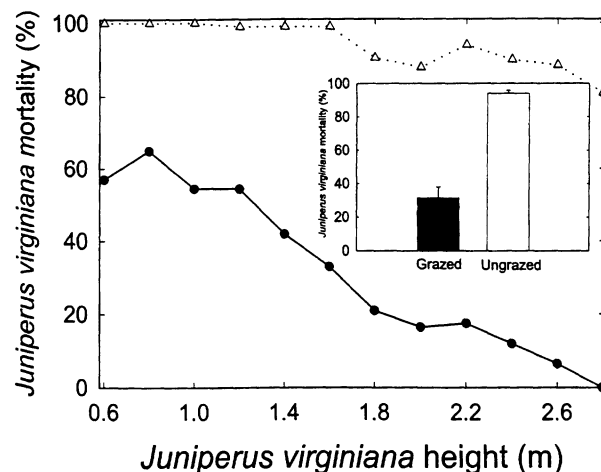
Figure 3. Relationship between densities of red cedar trees determined from point-quarter and species richness in a 10-m^2 circular plot. Data are from nine different sites with trees ranging in age from less than 10 years to 70 years. There was a significant inverse relationship between species richness and tree density ($r^2 = 0.56$, $P < 0.0001$; species richness $= 27.4 \bullet e^{(-0.0012 \bullet \text{tree density})}$. [1] Inset: The effects of red cedar canopy on herbaceous species richness in 10-m^2 plots. Plots outside the canopy had significantly higher levels of richness than plots under the red cedar canopy ($t = 17.01$, $P < 0.0001$). Data are from nine sites.

Figure 4. Eastern red cedar mortality from burning as a function of tree height on grazed (*closed circles*) and ungrazed (*open triangles*) tallgrass prairie. In two ungrazed sites, even the largest-size classes had a higher than 80% mortality rate. By contrast, the grazed sites had only a 50% mortality rate for trees in the 1-m class. Inset: Average red cedar mortality in grazed and ungrazed tallgrass prairie. Red cedars in ungrazed tallgrass prairie had significantly higher mortality rates than those located in ungrazed tallgrass prairie (ANOVA; $F = 210.4$, $P < 0.001$).

Discussion

Land-Cover Change—Forest Expansion

In the last 50 years, a widespread increase in forest cover has been noted throughout the eastern Great Plains states (Beilmann and Brenner 1951; Schmidt and Leatherberry 1995; Hoch and Briggs 1999). In the northern Flint Hills of Kansas, Abrams (1986) and Knight and others (1994) reported a substantial increase (54% in 46 years) in deciduous forest cover associated with riparian and/or deep soils. In the same area, closed-canopy red cedar forest has increased by 120% in 15 years (Hoch 2000). The more rapid expansion of red cedar forest may be related to its evergreen habit, the rapid growth rate of the tree, its high reproductive output, and its capability for widespread dispersal (Holthuizjen and Sharik 1985). Because red cedar forests can grow on thin, rocky soils (Table 1), the combination of deciduous and evergreen forest expansion on virtually all soil types represents a significant threat to the remaining tracts of tallgrass prairie.

A relatively rapid conversion of open grassland to a closed-canopy forest is not unique and has been documented elsewhere, although often nonnative rather than native tree species are involved. The invasion of the nonnative tree *Sapium sebiferum* into the Texas coastal prairie closely parallels the invasion of red cedar documented in this study. This species invades coastal prairie, where it rapidly suppresses the herbaceous species that provide the fine fuels necessary to carry a fire. Thus, when *Sapium sebiferum* achieves canopy closure, regardless of the height of the trees, the community is quickly rendered inflammable and fire can no longer be used to manage this species (Grace and others 2001). Red cedar forests in Kansas are similar; there does not appear to be enough fine fuel (0.18 g/m^2) in the understory to carry a fire under typical prescribed burning conditions.

Red Cedar Effects on Diversity and Productivity

The expansion of red cedar into tallgrass prairie had dramatic effects on the diversity and productivity of the grassland plant community (Figure 3). Beneath the red cedar canopy, virtually all grassland species were eliminated and richness was very low (Figure 3 inset)—often fewer than four species per 10-m^2 plot. In contrast, plots adjacent to red cedar stands had as many as 35 herbaceous species. Although there was no strong relationship between species richness and tree density at low tree density, our
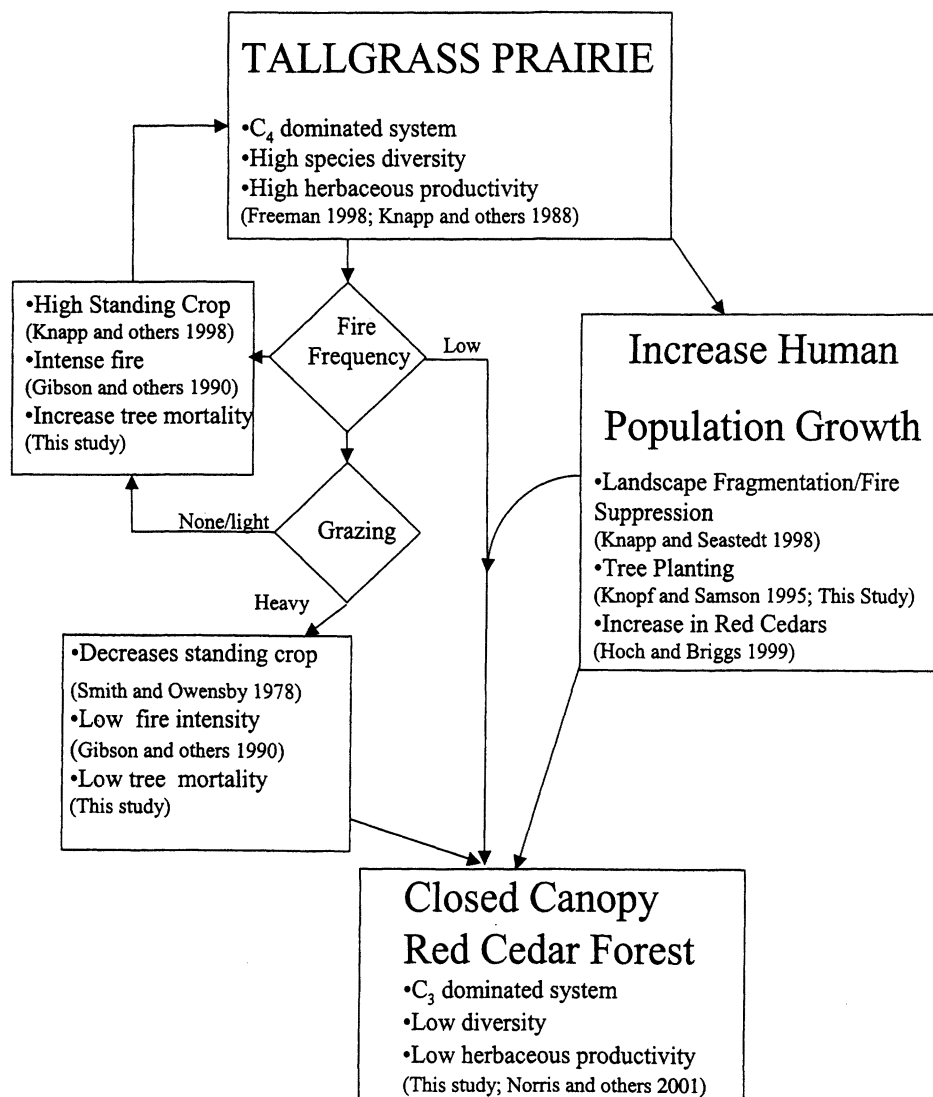
Figure 5. Conceptual model summarizing results from this research and previous studies that describe the general procedures by which native tallgrass prairie is being converted to close canopy red cedar forests. When fire is suppressed in the tallgrass prairie of northeast Kansas, red cedar forests expand at the expense of the tallgrass prairie. However, in grazed grasslands, where the fuel load is reduced, fires may not be able to control red cedars. Finally, fire suppression in the tallgrass prairie is being exacerbated by fragmentation of the landscape due to the increase in human population growth. The increase in human population can impact red cedars either directly (for example, by planting of trees) or indirectly, by increasing the fragmentation of the landscape. Fragmentation of the landscape decreases the frequency and intensity of fires. Both of these factors favor red cedars at the expense of tallgrass prairie. Thus, red cedar forests have multiple ways to increase in northeast Kansas, and the land-use practices that served to minimize red cedar expansion in the past may no longer be effective today.

data indicate that once trees achieved a density of approximately 1500 trees/ha almost all herbaceous species were eliminated.

In addition to reducing species richness, herbaceous productivity was reduced by more than 99% in the forest understory compared to annually burned tallgrass prairie at KPBS. Similarly, Engle and others (1987) and Schmidt and Stubbendieck (1993) measured a reduction in herbaceous productivity of 33%–96% under isolated red cedar trees growing in grasslands.

Causes of Land-Cover Change

The elimination of fire in tallgrass prairie is the primary reason closed-canopy red cedar forests have increased in the Great Plains grasslands (Briggs and Gibson 1992; Engle and Kulbeth 1992)

(Figure 5). The reduction of fire in this ecosystem can be directly linked to socioeconomic factors. In an earlier study, red cedar forest cover was positively correlated with human population growth and concurrent housing development in this region (Hoch and Briggs 1999). Fire, which previously occurred across broad landscapes, has since been greatly restricted or eliminated around developed areas as the landscape has become more fragmented (Knapp and Seastedt 1998). Further exacerbation of forest expansion is caused by direct activities of landowners who plant red cedar trees for landscaping, as windbreaks, or for wildlife habitat. In 1997 and 1998, the state of Kansas distributed 266,000 red cedar trees to the public (Kansas Forestry Extension Office).

A second major land-use factor that has been

linked to the increase of woody vegetation in North American grasslands is annual grazing by domestic ungulates (Figure 5). The importance and ecological value of grazers in the tallgrass prairie is unquestioned (Collins and others 1998; Knapp and others 1999). However, it is common practice in the Flint Hills for ranchers to graze their cattle into the late summer or early fall (Isern 1985). This management practice leaves little standing vegetation to support fires the following spring with sufficient intensity to kill red cedars (Figure 4). This practice sets up a feedback loop that promotes the growth and—more importantly—the establishment of woody species in the grasslands. Because the regional landscape today is a fragmented matrix of grazed lands and developed areas, there is an abundant red cedar seed source near virtually all remaining grasslands, increasing their vulnerability to red cedar establishment even when they are burned frequently. Thus, land-use practices that minimized red cedar expansion in the past may no longer be effective today. Other researchers across the world have reported similar phenomena (Brown and Carter 1998; Moleele and Perkins 1998; Dussart and others 1998). However, the interaction between grazing and fire intensity is the primary reason that woody species are invading and displacing grasslands worldwide.

ACKNOWLEDGMENT

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